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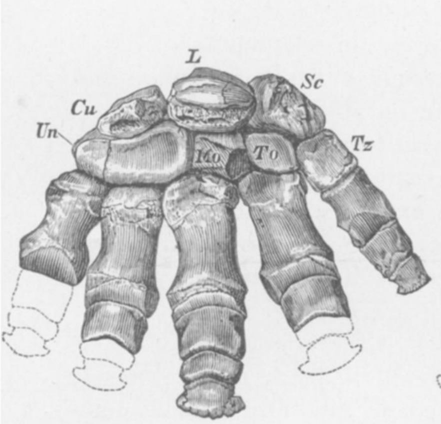
THE AMBLYPODA.

BY E. D. COPE.

THE Amblypoda is that order of hoofed mammals in which the internal bones of the carpus are in linear series, the magnum supporting a part of the lunar only, and not reaching the scaphoid; and in which the tarsal bones are interlocked, as in the later types of hoofed Mammalia; that is, the cuboid bone articulates extensively with the astragalus, as well as with the calcaneum (see Figs. 1–2).



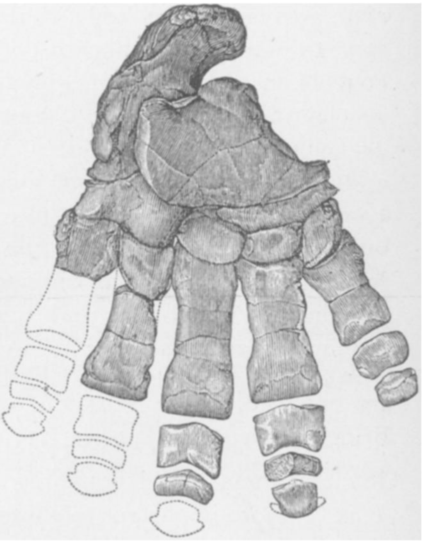


FIG. 1.—Right manus of Coryphodon. Original, from Proc. Amer. Philos. Society, 1882, p. 441. *Sc*, scaphoid; *L*, lunar; *Cu*, cuneïform (imperfect); *Tz*, trapezium; *To*, trapezoides; *Mo*, magnum (face broken); *Un*, unciform. From a New Mexican specimen. See Report U. S. G. G. Survey W. of 100th mer., IV, pl. LXI.

FIG. 2.—Right posterior foot of a species of Coryphodon from New Mexico, one-half nat. size. From Report Expl. W. of 100th mer., G. M. Wheeler, IV, pl. LIX.

Various other characters are associated with these, some of which may be coëxtensive with them, and therefore to be regarded as characters of the order. Thus all the known species have five toes on all the feet, and a flat astragalus without trace of groove. The unciform bone is extensively in contact with the lunar, as in the Diplarthra. The hemispheres of the brain are of singularly small size, and are separated from the olfactory lobes and from the cerebellum by their crura. The feet are always short and plantigrade.

Ordinal characters of wider significance are seen in the presence of a postglenoid process; the presence of enamel on the teeth, and the absence of any teeth growing from persistent pulps. The superior molar teeth are constructed on the tritubercular type.

Mammalia presenting the above combination of characters first appear in the Puerco Eocene epoch, and continue through the Wasatch and Bridger epochs, and then disappear. They have not been found in later deposits. The Puerco species are smallest in dimensions, while those of the Bridger epoch are the largest of Eocene Mammalia, equaling in the size of some of their bones the largest of living terrestrial Mammalia. Besides their great size the species of the Bridger epoch prove the ancient exuberance of their growth-energy in the development of extraordinary processes and horns on the head and large and formidable canine teeth.

Three suborders represent this order. Each one is confined to a distinct horizon of the Eocene period, with one doubtful exception. The characters are as follows:

Astragalus with a head; a third trochanter of femur; superior incisors.. *Taligrada.*
No head of astragalus; a third trochanter; superior incisors.......... *Pantodonta.*
No head of astragalus, nor third trochanter, nor superior incisors...... *Dinocerata.*

The Taligrada only occur in the Puerco epoch, the Pantodonta are confined to the Wasatch, and the Dinocerata belong to the Bridger epoch, one species having been found extending downwards into the Wasatch, unless there be some error.[1]

THE TALIGRADA.

The Taligrada are represented by one family, and one genus, Pantolambda Cope.[2] This form is interesting on various accounts. It furnishes the only known example of a tritubercular selenodont superior molar dentition. That is, each of the three cusps of which the crown of the superior molar is composed, is a well-formed V (Fig. 3 *a*). We shall see later on, that this form explains the origin of the peculiar molars of some of the Pantodonta. Its astragalus is of remarkable form, which is intermediate between that presented by the other members of the order, and the diplarthrous ungulates, as for instance, the rhinoceroses (Fig. 3, fig. *d d' d''*). It has the flat tibial face characteristic of all the Puerco mammals, and of many of those of the Wasatch

[1] This is the *Bathyopsis fissidens* Cope.

[2] See NATURALIST, 1883, p. 406.

epoch. The inferior molars are much like those of Coryphodon, but differ in certain details. The premolars are even more like those of that genus (Fig. 6). The humerus differs from that of all other members of the order in having an epicondylar foramen (Fig. 5 *a*). In this respect, and in its large internal epicondyle, the form is like that of some Creodonta. The ilium differs remarkably from that of the other genera of the order in its narrow form, with flattened triangular section, as is seen in various Rodentia. It approximates the Condylarthra in this respect also.

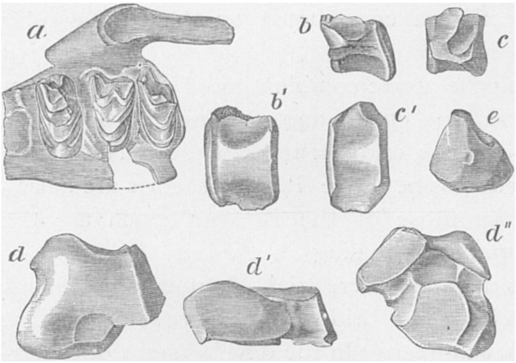


Fig. 3.—Bones and teeth of *Pantolambda bathmodon* Cope, two-thirds nat. size. From the Puerco beds of New Mexico. Fig. *a*, part of maxillary and malar bones from below, showing true molars, all somewhat broken. Figs. *b* and *c*, cervical vertebræ, left side; *b′* and *c′*, do. from below. Fig. *d*, astragalus from above; *d′*, from front, showing facet for cuboid; *d″*, from below; *e*, navicular bone from below. Original, from Report U. S. Geol. Survey Terrs., F. V. Hayden.

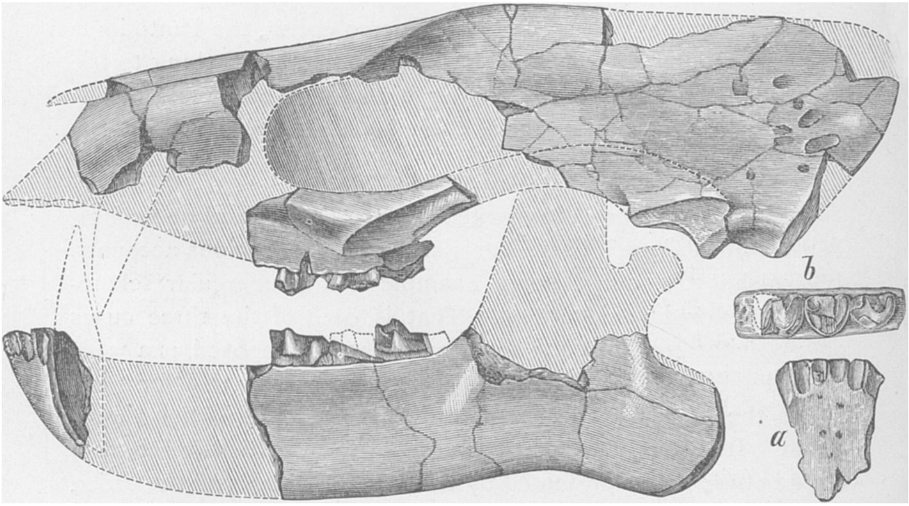


Fig. 4.—*Pantolambda bathmodon* Cope, skull, two-thirds nat. size. From the Puerco beds of New Mexico; individual represented in figs. 3 and 5. Fig. *a*, symphysis mandibuli from front. Fig. *b*, last two premolars and first true molar of inferior series from above, of a second individual. Original, from Vol. III Report U. S. Geol. Survey of Terrs., F. V. Hayden in charge.

In all respects Pantolambda presents primitive characters. The V shape of its molar tubercles only presents us with the highest known modification of the primitive tritubercular molar,[1] excepting those which succeeded it in time in the remaining suborders of the Amblypoda.

Of the genus Pantolambda two species have been discovered, both by Mr. David Baldwin, in New Mexico. The smaller of these, the *P. bathmodon* Cope (Fig. 4) is about the size of a coyote, the larger, *P. caviricius* Cope (Fig. 6) is as large as a South American tapir, or nearly equal to the smallest species of Coryphodon. The ungues of the *P. bathmodon* which have been found (Fig. 5 *c*) are narrower than those of the *P. caviricius*, but they may differ in proportions on different digits as in the species of Phenacodus. Both species are furnished with formidable canine teeth, but they are of normal form, and do not present any of the peculiarities of those of the Pantodonta or Dinocerata. In the lower jaw of the *P. caviricius* (Fig. 6) they are somewhat recurved, furnishing a formidable seizing and holding weapon. The lower edge of the mandibular

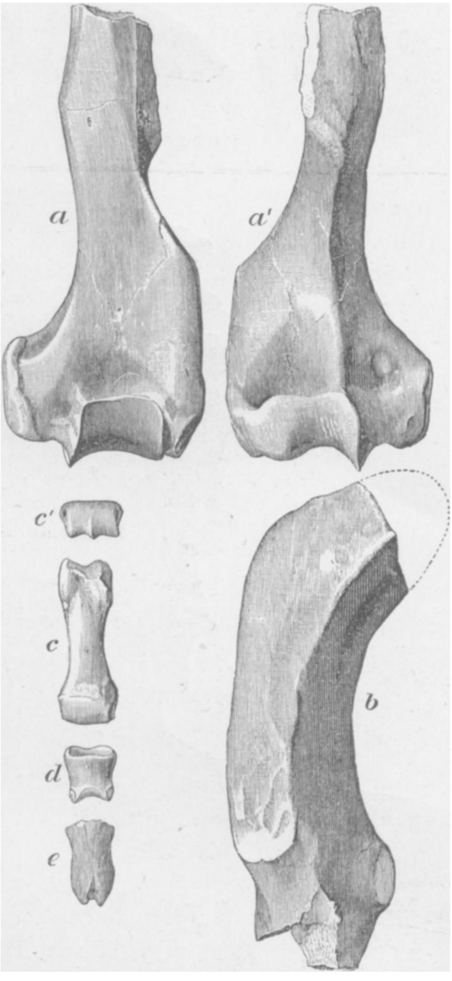


FIG. 5.—*Pantolambda bathmodon* Cope, bones of individual represented in figs. 3 and 4, two-thirds nat. size. Fig. *a*, distal half of humerus, posterior side; *a'*, anterior side. Fig. *b*, ilium from inner side. Fig. *c*, metapodial bone from front; *c'*, distal view; *d*, phalange; *c*, unguis. Original.

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[1] On this subject see Proceeds. Amer. Philos. Soc., 1883, p. 324.

ramus is prominent anteriorly, leaving a concavity of the lateral face posterior to the root of the canine. This resembles a good deal what is seen in the cat-like genus Nimravus and allies, which are probably the ancestors of the saber-tooth tigers. The corresponding form in Pantolambda in the same way foreshadows the great development of mandibular flange, and of the superior canine, seen in the Dinoceratous group of this order.

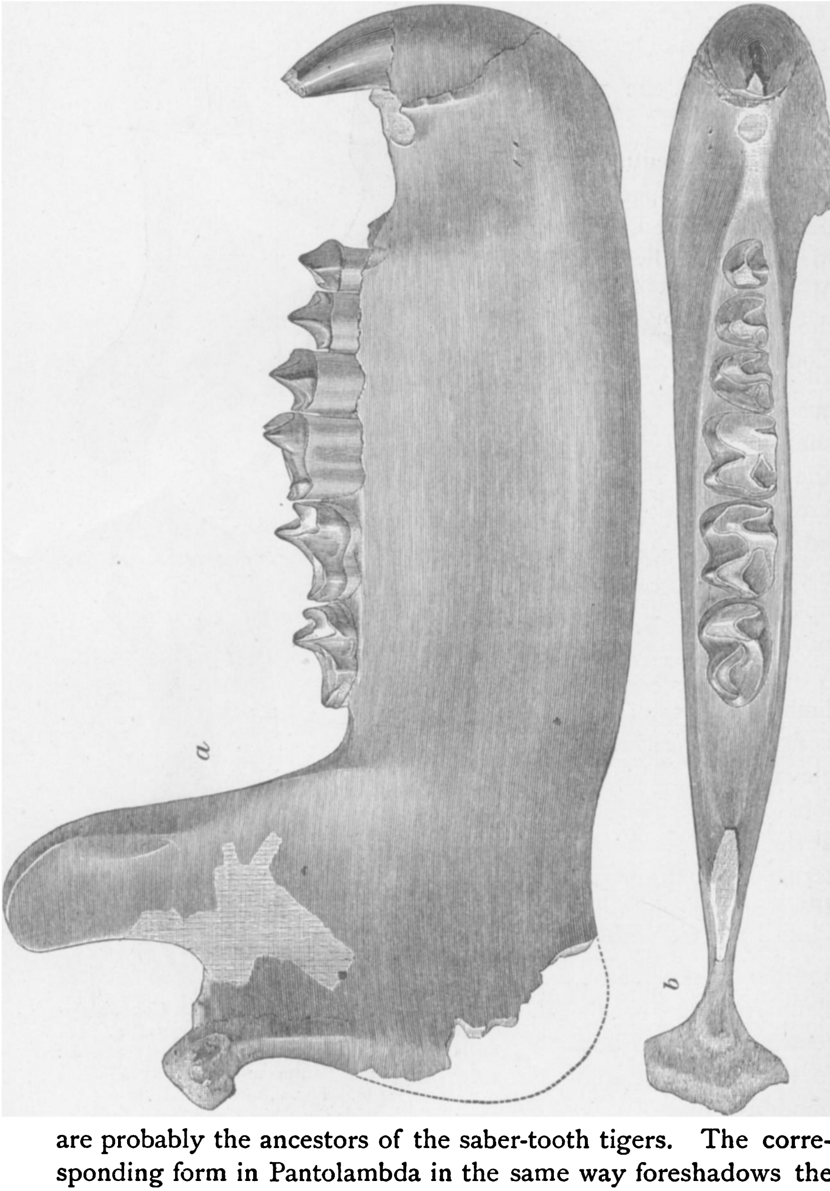

FIG. 6.—*Pantolambda cavirictus* Cope, mandibular rami, two thirds natural size. Fig, *a*, right ramus for outer side. Fig. *b*, left ramus from above. From Puerco bed. Original, from Vol. III Report U. S. Geol. Survey Terrs., F. V. Hayden in charge.

The homologies of the parts of the teeth of the different genera of the Amblypoda are not determined without considerable study. The greatest difficulties are presented by the superior molars, and in order to understand them it is necessary to study the inferior molars first.

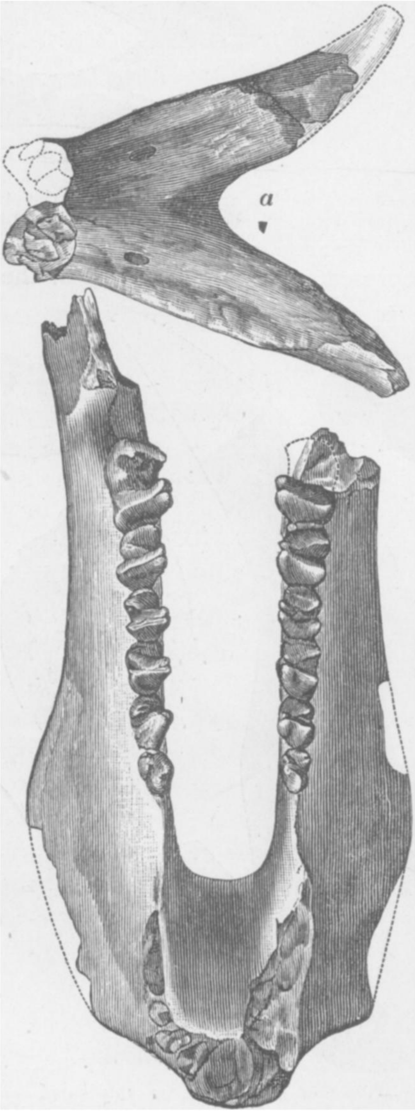

FIG. 7.—*Bathyopsis fissidens* Cope (one of the Dinocerata), mandible anterior to the coronoid process; incisors and canines and first premolar lost from both sides, two-thirds nat. size, from above; *a*, from front. Original, from Wind River (? Bridger) of Wyoming. From Vol. III Report U. S. Geol. Survey Terrs., F. V. Hayden.

If we compare the inferior molars of the *Pantolambda cavirictus* with those of the *Bathyopsis fissidens* (Fig. 7) (one of the Dinocerata) the following modifications will be observed: (1) The two limbs of the anterior V in the true molar of the former are represented in the latter by a single crest with two appressed apices at the inner extremity. These apices represent those of the two limbs of the V. (2) The posterior limb of the posterior V is much diminished in elevation, and does not join its anterior limb at the apex on the external side of the crown. If we now examine the corresponding parts of another Dinoceratous Amblypod, a species referred by Mr. Osborn to the genus Loxolophodon (Fig. 8), we find the process carried still further. The crown has only two crests which approach each other but do not join at the apex on the inner side. The posterior limb of the posterior V has disappeared, and a small cusp represents the posterior crest of the anterior V.

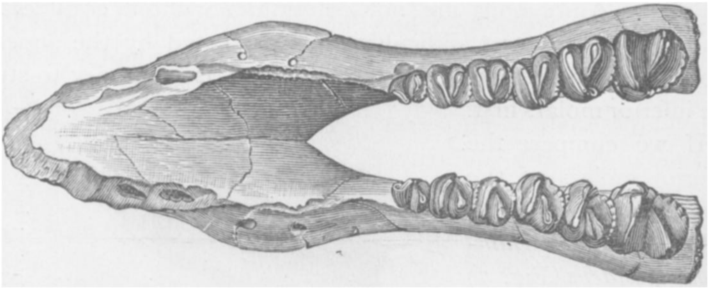

FIG. 8.—Loxolophodon sp., mandible anterior to coronoid process, one-fourth nat. size; from Bridger beds of Wyoming. From Osborn, memoir on Loxolophodon and Uintatherium.

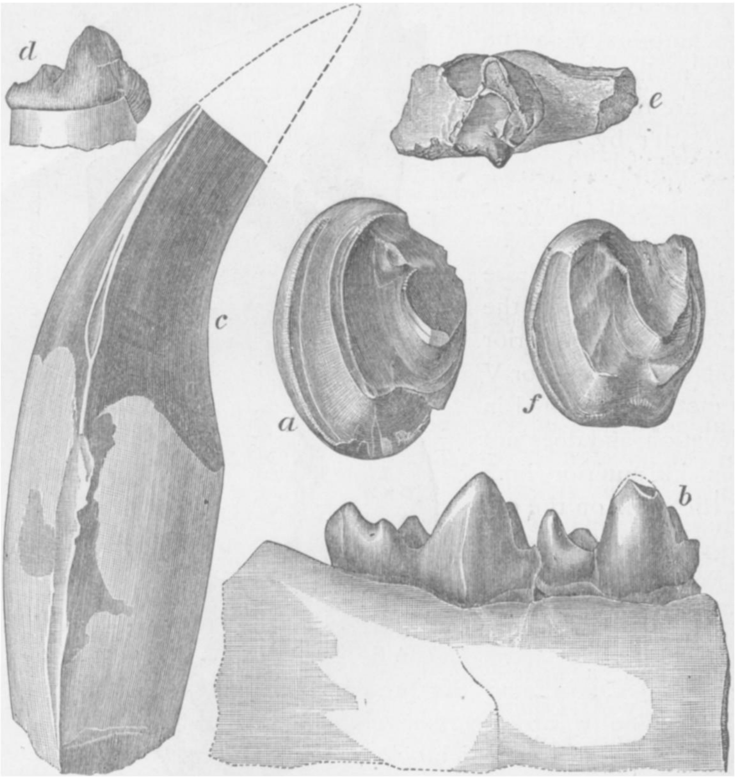

FIG. 9.—Teeth of Pantodonta, two-thirds nat. size. Figs. *a–d*, *Coryphodon anax* Cope; from the Wasatch beds of Wyoming. Original, from Vol. III Report U. S. Geol. Surv. Terrs. Fig. *e*, *Coryphodon cuspidatus* Cope, last inferior molar from above, anterior V broken; from New Mexico. Report U. S. G. G. Survey W. of 100th mer., G. M. Wheeler, original. Fig. *f*, last superior molar of *Manteodon quadratus* Cope, from below; from Wyoming. Original, from Vol. III Report U. S. Geol. Surv. Terrs., F. V. Hayden in charge.

Let us now compare the superior molars of Pantolambda (Fig. 3) with those of Coryphodon (Fig. 9 *a*). The two external Vs of the former are represented in the latter by a cusp and a partial V, which form an oblique ridge on the external half of the posterior side of the tooth. This arrangement is already imitated on the last molar of Pantolambda, where one of the Vs has disappeared, and the one that remains is very oblique.

The second V preserves its form better in the superior molar of *Manteodon quadratus* (Fig. 9 *f*); while in the genus Metalophodon Cope, it is reduced to a cusp, forming the inner extremity of a transverse crest. (A figure of this genus will be given in the next number of the NATURALIST.) The interior V of Pantolambda is represented by a corresponding angle at the inner side of the crown in Coryphodon (Fig. 9 *a*), and the two ridges which connect it with the external base of the crown are well marked. Besides these there is developed on the anterior side of the base a strong cingulum. This is wanting on the posterior side, but is present in a feeble form in Pantolambda (Fig. 3). I have sometimes called these the superior and inferior anterior cingula respectively. In Coryphodon the posterior superior cingulum is unsymmetrically bulged near its interior end, and in Manteodon it develops a cusp at this point, the crown thus becoming quadritubercular (Fig. 9 *f*).

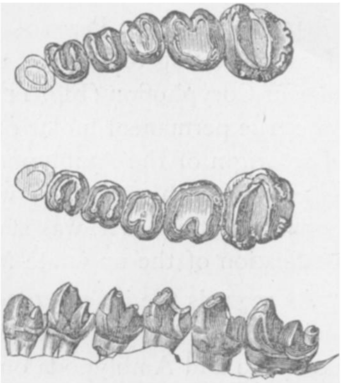

FIG. 10.—Dinocerata teeth, one-fourth nat. size. Upper figures superior molars of *Uintatherium leidianum*, one-fourth nat. size. Lower figure, inferior molars of jaw of Loxolophodon represented in fig. 8. From Osborn, memoir on Uintatherium and Loxolophodon.

If we now compare these teeth with those of Uintatherium (Fig. 10) we have little difficulty in determining the presence of the two anterior cingula. The difficulty is to ascertain the homology of the posterior transverse crest. It is difficult to see in it the two external Vs of Pantolambda confluent into a simple ridge, yet such it seems to be. This will be especially clear on comparison with the figure of Metalophodon. One is tempted to compare it with the posterier superior cingulum of Coryphodon, but the frequent presence of a cusp posterior to its internal extremity in the Dinocerata presents a further obstacle to such a determination. This cusp is probably homologous with the posterior internal tubercle of Manteodon (Fig. 9*f*), and is, therefore, the posterior internal of the quadrituberculate molar type. The internal extremity of the posterior crest of the crown in the Dinocerata cannot, therefore, be that cusp, and that ridge is not a posterior transverse crest, such as is present in most Perissodactyla.

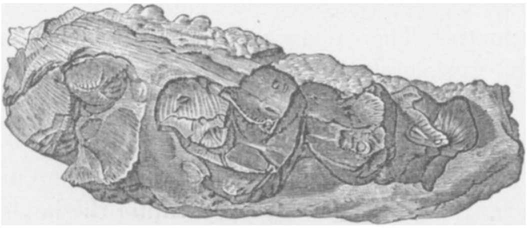

FIG. 11.—Last three temporary molars, and first true molar partly protruded, of a Coryphodon from New Mexico, nat. size. Original, from Report U. S. G. G. Survey W. of 100th mer., G. M. Wheeler, Vol. IV, pt. II.

It is interesting to observe that the fourth superior deciduous molar in Coryphodon (Fig. 11) has essentially the same structure as the true permanent molar of Pantolambda (Fig. 3).

The origin of the Amblypoda has not yet been traced. What was known on this point, as well as on the question of the descendants of the order, was stated as follows in my paper on the classification of the ungulate Mammalia, published in 1882:[1]

" As regards the inner part of the manus, I know of no genus which presents a type of carpus intermediate between that of the Taxeopoda and Amblypoda on the one hand, and the Perissodactyla and Artiodactyla on the other. Such will, however, probably be discovered. But the earliest Perissodactyla, as for instance Hyracotherium, Hyrachyus and Triplopus, possess the carpus of the later forms, Rhinoceros and Tapirus. The order Amblypoda occupies an interesting position between the two groups, for while it has the carpus of the primitive type, it has the tarsus of the later orders. The bones of the tarsus alternate, thus showing a decided advance on the Taxeopoda. This order is then less primitive than the latter, although in the form of its astragalus it no doubt retains some primitive peculiarities which none of the

[1] Palæontological Bulletin No. 35. Proceedings Amer. Philosoph. Society, 1882, p. 445.

known Taxeopoda possess. I refer to the absence of trochlea, a character which will yet be discovered in the Taxeopoda, I have no doubt.

"The Taxeopoda approach remarkably near the Bunotheria, and the unguiculate and ungulate orders are brought into the closest approximation in these representatives. In fact I know of nothing to distinguish the Condylarthra from the Mesodonta, but the ungulate and unguiculate characters of the two divisions. In the Creodonta this distinction is reduced to very small proportions, since the claws of Mesonyx are almost hoofs. Some of the genera of the Periptychidæ present resemblances to the Creodonta in their dentition also.

"The facts already adduced throw much light on the genealogy of the Ungulate Mammalia. The entire series has not yet been discovered, but we can with great probability supply the missing links. In 1874 I pointed[1] out the existence of a yet undiscovered type of Ungulata, which was ancestral to the Amblypoda, Proboscidea, Perissodactyla and Artiodactyla, indicating it by a star only in a genealogical table. This form was discovered in 1881, seven years later, in the Condylarthra. It was not until later[2] that I assumed that the Diplarthra are descendants of the Amblypoda, although not of either of the known orders, but of a theoretical division with bunodont teeth.[3] That such a group has existed is rendered extremely probable in view of the existence of the bunodont Proboscidea and Condylartha. That the Taxeopoda was the ancestor of this hypothetical group, as well as of the Proboscidea, is extremely probable. But here again neither of the suborders of this group represent exactly the ancestors of the known Amblypoda, which have an especially primitive form of the astragalus not found in the former. In the absence of an ankle joint the Amblypoda are more primitive than any other division of the Ungulata, and their ancestors are not likely to have been more specialized than they. It is probable that a third suborder of Taxeopoda has existed which had no trochlea of the astragalus, which I call provisionally by the name of Platyarthra.

"The preceding paragraphs were written in May, 1882. On my return home, September 1st, after an absence of three months, I find that various parts of the skeleton of Periptychus have reached my museum.[1] On examination I find that the astragalus of that genus fulfills the anticipation above expressed. *It is without trochlea*, and nearly resembles that of Elephas. As it agrees nearly with that of Phenacodus in other respects, I only separate it as a family from the Phenacodontidæ. One other type remains to be discovered which shall connect the Periptychidæ and the hypothetical Hyodonta, and that is a taxeopod without a head to the astragalus—unless, indeed, the 'Hyodonta' should prove to have such a head. I think the latter the less probable hypothesis, and hence retain the term Platyarthra for the hypothetical taxeopod without trochlea or head of the astragalus." This group as at first defined had been already discovered, but in the above paragraph I added another definition, endeavoring to preserve an apparently useless name.

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[1] Homologies and Origin of Teeth, etc., Journal Academy Nat. Science, Philada., 1874, p. 20.

[2] Report U. S. Geol. Survey W. of 100th mer., p. 582, 1877.

[3] This hypothetical suborder has been called Amblypoda Hyodonta.

The existence of Amblypoda Hyodonta is rendered almost certain by the discovery that the genus Pantolestes of the Wasatch epoch is an artiodactyle with tritubercular bunodont superior molars. The ancestral type of such a form must have been a tritubercular bunodont amblypod. Pantolambda is such a form with the tubercles modified into Vs. Moreover, such a type (Amblypoda Hyodonta) would be derived from a periptychid Taxeopod with but little modification of the latter. A distinct faceting of the astragalus for the cuboid bone, and *probably* a change of the carpus by an articulation of the unciform and lunar bones, would be all that would be necessary. The discovery of Pantolambda has increased the probability of such change having taken place in the hind foot, since *the astragalus is intermediate in form between those of Coryphodon and Periptychus.* This is particularly seen in the form of the head, which is not separated by a neck as in Periptychus, but is more prominent than in other Amblypoda (Fig. 3). Thus it is possible that Amblypoda Hyodonta will be found to have a short head of the astragalus, contrary to my supposition above expressed. The headless astragulas of other Amblypoda and of Proboscidea is perhaps a derivative and not a primitive character.

The following diagram gives expression to these views as to the phylogeny of the ungulates. It is the same that I published in 1882 in the paper above quoted, modified so as to be more intelligible:

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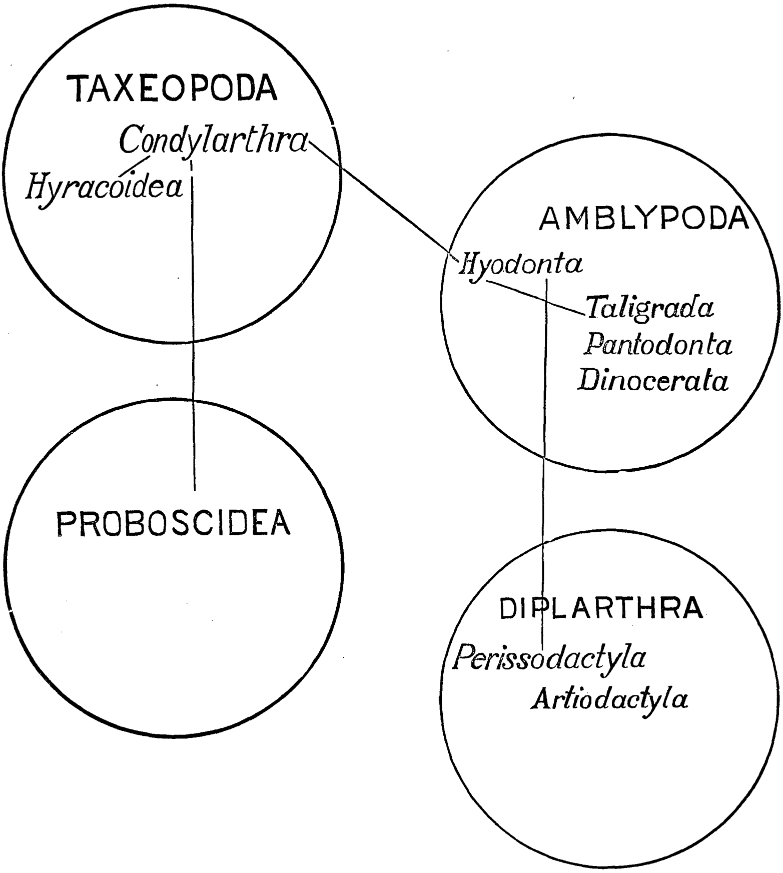
[1] See NATURALIST for August, 1884, for figures.



(*To be continued.*)

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EDITORS' TABLE.

EDITORS: A. S. PACKARD AND E. D. COPE.

—— The American Association for the Advancement of Science met this year in Philadelphia, between September 4th and 11th, inclusive. Omitting Saturday, which was given up to excursions, and Sunday, there were six and a-half days of work. The first of these was devoted to the addresses of welcome, and those of the vice-presidents, or chairmen of the sections. The